

Yucca brevifolia fruit production, predispersal seed predation, and fruit removal by rodents during two years of contrasting reproduction¹

Mark I. Borchert^{2,4} and Lesley A. DeFalco³

PREMISE OF THE STUDY: The distribution of *Yucca brevifolia*, a keystone species of the Mojave Desert, may contract with climate change, yet reproduction and dispersal are poorly understood. We tracked reproduction, seed predation, and fruit dispersal for two years and discuss whether *Y. brevifolia* is a masting species.

METHODS: Fruit maturation, seed predation (larval yucca moths), and fruit dispersal (rodents) were monitored on a random sample of panicles during 2013 and 2014, which were years of high and low reproduction, respectively. Fates of fruits placed on the ground and in canopies were also tracked. Rodents were live-trapped to assess abundance and species composition.

KEY RESULTS: In 2013, 66% of inflorescences produced fruit of which 53% escaped larval predation; 19.5% of seeds were destroyed in infested fruits. Total seed production was estimated to be >100 times greater in 2013 than 2014. One-third of the fruit crop fell to the ground and was removed by rodents over the course of 120 d. After ground fruits became scarce, rodents exploited canopy fruits. Rodent numbers were low in 2013, so fruits remained in canopies for 370 d. In 2014, fruit production was approximately 20% lower. Larvae infested the majority of fruits, and almost twice the number of seeds were damaged. Fruits were exploited by rodents within 65 d.

CONCLUSIONS: High fertilization, prolific seed production, and low predispersal predation in 2013 suggests that pollinator attraction and satiation of seed predators influence masting in *Y. brevifolia*. Abundant, prolonged fruit availability to seed-dispersing rodents likely extends recruitment opportunities during mast years.

KEY WORDS Joshua tree; *Yucca brevifolia*; masting; fruit production; Mojave Desert; fruit removal; pre-dispersal seed predation; *Ammospermophilus leucurus*; desert rodents

Yucca brevifolia Englem. (Joshua tree) is perhaps the most recognizable living symbol of the Mojave Desert. In the late Pleistocene, this arborescent yucca was widely distributed in most of southeastern California, southern Nevada, southwestern Arizona, and northern Mexico (Cole et al., 2011). Warming during the Holocene caused its range to contract northward into the present-day archipelago of large, disjunct patches scattered across eastern California, southern Nevada western Arizona, and southwestern Utah (Cole et al., 2011). According to climate models, the current distribution of

Y. brevifolia is predicted to shrink even further as the Southwest deserts continue to warm (Dole et al., 2003; Kerr, 2008; Cole et al., 2011; Barrows and Murphy-Mariscal, 2012).

Plant mortality is expected to be high in Joshua Tree National Park at the southern edge of its range, although expansion into central Nevada may compensate for some of these losses (Cole et al., 2011). This range shift and potential losses of *Y. brevifolia* have prompted a flurry of studies on the ecology of this species including: demography (Gilliland et al., 2006; Esque et al., 2010; Esque et al., 2015), fire ecology (Loik et al., 2000; DeFalco et al., 2010; Vamstad and Rotenberry, 2010), seed dispersal (Vander Wall et al., 2006; Waitman et al., 2012), and seedling establishment (Brittingham and Walker, 2000; Reynolds et al., 2012). In contrast, the reproductive ecology of *Y. brevifolia* has been little studied even though there is evidence that climate change may be decreasing fruit production

¹ Manuscript received 8 December 2015; revision accepted 11 March 2016.

² San Bernardino National Forest, P.O. Box 292, Fawnskin, California 92333; and

³ U.S. Geological Survey, Western Ecological Research Center, 160 N. Stephanie St., Henderson, Nevada 89074

⁴ Author for correspondence (e-mail: borchert1@charter.net)
doi:10.3732/ajb.1500516

in desert species such as pinyon pine (*Pinus edulis*) (Redmond et al., 2012).

Yucca brevifolia is known to have episodes of large, synchronous seed crops that are heavily preyed on by small mammals—attributes that may have selected for a masting reproductive strategy. Compared with a strategy of producing a low but predictable seed crop, masting has the selective advantage of satiating predators and reducing seed losses (Kelly, 1994; Vander Wall, 2002). Masting has been linked to environmental cues that synchronize reproduction. For example, high antecedent rainfall in arid regions of Australia triggers the mass reproduction of fire-adapted species (Wright and Zuur, 2014; Wright et al., 2014). However, the proximate causes of mast years may be more complicated than simple resource matching, particularly for species that inhabit arid environments where vegetation is not fire-adapted (Meyer and Pendleton, 2015). Masting in unproductive environments may be less tied to environmental cues. In desert environments the replenishment of stored resources necessary for producing large seed crops may take longer to accumulate than in productive environments where resources are more readily available (Kelly and Sork, 2002).

Several hypotheses have been proposed to explain masting in plants that exhibit high variation in reproduction (Kelly, 1994). Hypotheses relevant to *Y. brevifolia* include: (1) higher fertilization associated with greater attraction of pollinators (animal pollination hypothesis), (2) lower seed predation because high seed production satiates predators (predator satiation hypothesis), and (3) higher seed dispersal or greater dispersal distances because large fruit seed crops attract a wider array of seed dispersing species (animal dispersal hypothesis).

Yucca brevifolia produces seeds in large, nonfleshy, indehiscent fruits (berries). Seed dispersal depends exclusively on rodents that open fruits and extract seeds for immediate consumption or caching for later use (Vander Wall et al., 2006; Waitman et al., 2012). Although masting has been well described in wind-pollinated species (Kelly, 1994), *Y. brevifolia* depends exclusively on yucca moths of the genus *Tegeticula* for pollination (Pellmyr, 2003), although their larvae also cause seed losses by consuming a portion of the seed crop. Thus, in addition to mass floral displays attracting pollinating moths, both pre- and postdispersal seed predation may select for masting in *Y. brevifolia*.

Flowering and fruit production by *Y. brevifolia* have been characterized as irregular (Esque et al., 2010) with large reproductive events averaging twice per decade (DeFalco and Esque, 2014). In 2013, *Y. brevifolia* flowered profusely over its entire range (James, 2013) although reproduction was generally lower in the following year. These contrasting years were the impetus for a study of fruit and seed production, seed predation, and fruit losses for this species at a site in the western part of its range. The goal of this study was to compare flowering and fruiting in *Y. brevifolia*, predispersal seed predation by moth larvae, and postdispersal fruit removal by rodents in high- and low-reproduction years.

Although a long-term study is necessary to formally test for the evolutionary drivers regulating interannual variation in flowering and seed production in *Y. brevifolia*, this study explores whether flower/fruit production and fruit dispersal during two contrasting years are consistent with animal pollination, predator satiation, and/or animal dispersal hypotheses that would explain the selection of masting as the reproductive strategy for this unique desert species.

MATERIALS AND METHODS

Study area—The study was conducted in a 10.2-ha area approximately 6 km north northeast of Big Bear City, California (34°15.97'N, 116°50.55'W) in the high desert of the San Bernardino Mountains. Elevation of the study area is 1776 m. Topography is gently sloping (slopes average < 5°) and soils are coarse gravelly sands derived from granite. Shrubs such as *Lycium* spp., *Fremontodendron californicum*, *Artemisia tridentata*, *Ceanothus vestitus*, and *Purshia tridentata* var. *glandulosa* dominate the vegetation with an average cover of 33%. *Yucca brevifolia* cover is 9.6%, and it typically grows in stands of individuals of many different heights. The study area is surrounded by *Pinus monophylla* woodlands, but fewer than 15 small pinyon trees grow in the study area. There is no documented occurrence of fire in the area since 1910 when records first began (fire history maps, Supervisor's Office, San Bernardino National Forest), although a wildfire burned in the southwest edge of the study area in 1946.

Climate of the study area is Mediterranean, which is characterized by cold, wet winters and warm, dry summers. Long-term (1985–2014) average annual precipitation based on a spatial interpolation of regional climate stations (PRISM Climate Group, Oregon State University, Website <http://prism.oregonstate.edu> created 6 July 2015) is 313 ± 145 mm, most of which falls as snow from November to April although the study area occasionally experiences ephemeral summer and fall rainfall events. Both years of the study occurred during prolonged drought. Annual precipitation during the study was 136 mm in 2013 (43% of the average) and 255 mm (81% of the average) in 2014.

Predispersal seed predation by moth larvae—In the latter part of May, fertilized, nonaborted flowers produce small, narrow green fruits that grow rapidly if they do not abort. When fruits reach full size, they are green, firm, and strongly attached to the panicle. We expected fruits reaching full size to be mature, which is consistent with the observations of Lenz (2001): "...at this stage, the endocarp is green, to some extent comparable to the flesh of a kiwi fruit. The seeds are mature and capable of germination beginning within 24 hours". In both years we collected a random sample of 75 green, full-sized fruits just before they began to dry. We cut them from the panicle with shears or twisted them multiple times to break the fibrous peduncle.

We collected fruits on 26 June 2013 and on 2 July 2014 and weighed each fruit after measuring its length and maximum width, and then excised each of six locules from the fruit. The length of each locule was measured, moth (*Tegeticula synthetica*) larval infestation was recorded, and undamaged seeds were counted. Undamaged seeds showed no signs of larval consumption. In contrast, larvae damaged seeds by eating holes through the centers of seeds or by consuming the edges. Seeds eaten by larvae often were in small pieces, or in the early stages of development. Thus, it was not possible to count damaged seeds in each locule.

Inflorescence and infructescence densities—We selected 50 random points in the study area in 2013 and 2014. A different set of random points was selected each year. At each point, we counted the number of inflorescences and infructescences in 400 m² (circle with a radius of 11.28 m).

Fruit density and fruit removal—During the first week of June in both years, we chose 50 random infructescences and counted the number of full-sized, green fruits and measured the height of each infructescence above the ground. Beginning on 4 June 2013, we

counted the number of fruits on each infructescence and again every 10 d for the first 90 d. Thereafter, fruits were counted every 20 d until they disappeared. We followed the same protocol in 2014, but counts began a month earlier on 6 May 2014, and were counted every 14–15 d until they were gone. A photograph of each panicle was taken to estimate its angle from vertical.

At each census, we categorized fruits as follows: attached to the panicle, opened by rodents, dispersed from the canopy by rodents, fallen into the rosette of upturned leaves below the panicle, impaled on leaf tips, and natural fruit fall. Opened fruits had remnants still attached to the peduncles, as well as partially opened fruits trapped in the leaf rosettes. Initially, opened fruits contained some unremoved seeds, but they disappeared over time. To calculate the number of fallen fruits or those taken from the canopy by rodents, we summed the number of attached fruits, those in the rosette, those opened by rodents, and those impaled on leaf tips and subtracted this total from the sum of the attached, rosette, and impaled fruits of the previous census.

Experimental removal of ground and elevated fruits—On 14 July 2013, we placed a single fruit on the ground below each of 50 random trees. A wooden marker was placed next to the fruit to distinguish it from fallen fruit. In addition, we impaled a fruit on a leaf tip 50 cm above each ground fruit. The disappearance of these elevated fruits signaled that rodents had climbed into the canopy to remove fruits. Every 20 d, we noted whether ground or elevated fruits were still present. We repeated this protocol in 2014 for fruits deployed on 13 July.

Live-trapping—In the center of the 10.3-ha study area, we established a 6 × 6 live-trap grid with 35-m spacing between traps (3.06-ha grid). We placed one 10.2 cm × 11.4 cm × 38.1 cm Sherman live trap under a shrub or tree within 1 m of each station marker. Cotton batting was placed at the back of the trap for insulation, and black oil sunflower seeds were provided as bait.

In 2013, we trapped for four days and nights (144 trap nights) beginning 23 July. Traps were checked in the morning before 1000 h and again at 1700 h. In 2014, trapping began on 18 September, two months later than in 2013. Captured individuals were identified to species and marked with a permanent marking pen, but no attempt was made to identify individual rodents of each species.

Statistical analyses—Densities of inflorescences and infructescences were not normally distributed, so we carried out between-year comparisons with Mann-Whitney *U* tests. We used a *z*-test to compare fruits per infructescence. Analysis of covariance was used for between-year comparisons of undamaged seeds per uninfested fruits, and undamaged seeds per infested fruits. The response variable was the number of uninfested seeds, the independent variable was whether the fruit was infested or not, and the covariate was locule length. Experimental ground and elevated fruit removal was analyzed using Kaplan-Meier survival analysis. Survival was estimated as the proportion of fruits surviving each 20-d period. Survival curves for ground and elevated fruits were compared using a log-rank test.

RESULTS

Trapping results—Four times more individuals, and a wider array of rodent species, were captured in 2014 than in 2013 (Table 1).

TABLE 1. Number of unique individuals of each rodent species captured during 2013 and 2014.

Species	2013	2014
White-tailed antelope squirrel	5	18
Pinyon mouse	2	23
Merriam's kangaroo rat	4	5
Desert woodrat	0	4
Agile kangaroo rat	1	0
California ground squirrel	0	1
San Diego pocket mouse	0	1
Merriam's chipmunk	0	1

White-tailed antelope squirrels (*Ammospermophilus leucurus*), pinyon mice (*Peromyscus truei*) and Merriam's kangaroo rats (*Dipodomys merriami*) were the most common species captured each year. Of the species listed in Table 1, white-tailed antelope squirrels, pinyon mice, California ground squirrels (*Otospermophilus beechyi*), desert woodrats (*Neotoma lepida*), and Merriam's chipmunks (*Eutamias merriami*) can climb *Y. brevifolia* to collect fruits. Merriam's kangaroo rats, agile kangaroo rats (*Dipodomys agilis*), and the San Diego pocket mouse (*Chaetodipus fallax*) are not known to climb, but they open fallen fruits. Of these species, white-tailed antelope squirrels, California ground squirrels, and Merriam's chipmunks are diurnal.

Phenology of fruit development—Fruits reached full size during the last week of May in both years. In contrast to our expectation, seeds were white and immature and it was not until ~14 d after fruits reached full size that seed coats turned black and were capable of germination (Lenz, 2001; Waitman et al., 2012; Reynolds et al., 2012). Rodents consumed few fruits during this 14-d seed maturation period. In fact, white-tailed antelope squirrels frequently gnawed the exocarp without opening the fruit, perhaps to detect when seeds were ripe. Once green fruits developed black seeds, rodents opened fruits while they were still firmly attached to the panicle.

As attached fruits dried (whether opened by rodents or not), they turned from pale green to a whitish, light-brown color with dark brown lining the locule fissures. During this 30-d transition period, the mesocarp softened and the peduncle dried and weakened. Still high in moisture content, fruits dropped to the ground of their own weight or into the rosette of leaves below the panicle. Other fruits remained attached to the panicle as they dried and were opened by rodents or removed by them over time (Fig. 1).

Fruit production—The density of inflorescences was more than three times higher in 2013 than in 2014 ($z = 2.08$, $P = 0.04$), and a higher percentage of inflorescences produced fruits in 2013 than in 2014 (Table 2). Infructescence density in 2013 was five times higher than in 2014 ($z = 5.40$, $P < 0.001$). Fruits per infructescence also were significantly higher in 2013 than in 2014 ($z = 6.12$, d.f. = 1, 98, $P < 0.001$) (Table 2).

Predispersal fruit and seed predation—Undamaged seeds in infested fruits were significantly higher in 2013 than in 2014 ($F_{1,93} = 28.0$, $P < 0.001$), as were seeds in uninfested fruits ($F_{1,50} = 65.1$, $P = 0.03$) (Table 3). Consequently, more undamaged seeds were produced per fruit in 2013 than in 2014. In addition, in 2013, 53% of the fruits were uninfested by larvae compared to 17% in 2014. Overall, seed predation by moth larvae was more than two times higher in 2014 than in 2013 (Table 3).

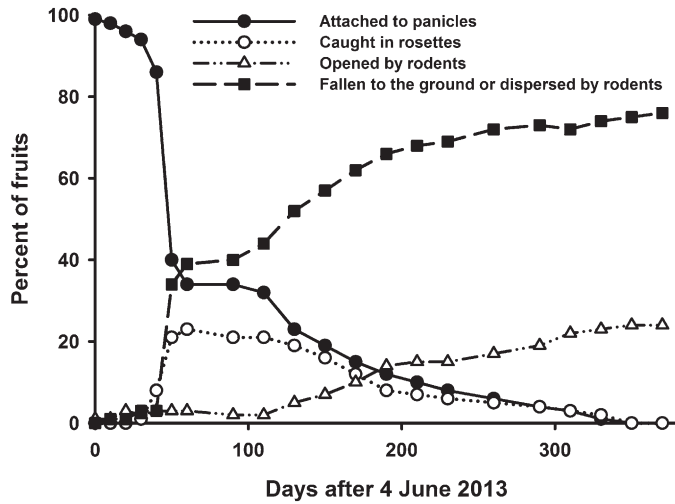


FIGURE 1 Fates of fruits attached to panicles, fallen into rosettes, opened by rodents, or dispersed by rodents during the high reproduction year of 2013. Impaled fruits are not shown (comprised $\leq 2\%$ of the fruits) for clarity. Percentages are calculated based on 1401 fruits counted on 4 June 2013.

Fate of fruits attached to the infructescences—On 4 June 2013, we counted 1401 attached fruits on 50 infructescences. Fruits declined minimally in the first 40 d (Fig. 1). Between 40 and 50 d there was a sudden, heavy fruit fall (Fig. 1), the result of the mesocarps softening and fruits pulling away from the peduncles. In this 10-d period 294 fruits (73%) detached from the drying panicles. Of this total, 34% fell to the ground or dropped into the leaf rosettes (22%). A small percentage (2%) was impaled on leaf tips or fell into the canopies of understory shrubs. Around 110 d, the remaining attached fruits continued a gradual decline from 32 to 0% by the end of the census period (370 d, Fig. 1). White-tailed antelope squirrels (unpublished camera trapping) removed fruits from the canopy although a small number fruits likely were dislodged from the panicles or rosettes and knocked to the ground. In addition, by the end of the study, about 18% of the remaining attached fruits were opened or dispersed from the canopy by rodents, although some fell into the rosettes after absorbing moisture from occasional summer rains. Opening and removal of rosette fruits began about the same time as the removal and opening of attached fruits (Fig. 1).

In 2014 we counted 445 fully developed fruits on 6 May. In contrast to 2013, all the fruits were opened or taken from the canopy within 65 d, well before they dried completely. In contrast to 2013, none fell to the ground or into leaf rosettes (Fig. 2). Although fruit and seed production and rodent numbers differed markedly between the two years, the percentage of fruits opened by rodents was similar: 24% in 2014 and 28% in 2014 (Figs. 1 and 2).

Disappearance of experimentally placed ground and elevated fruits—The survival of ground- and elevated fruits in 2013 were significantly different from one another based on the log-rank test ($\chi^2 = 59.2$, d.f. = 1, $P < 0.001$). Ground-fruit survival dropped almost 60% 50 d after deployment and they disappeared after 120 d (Fig. 3). Elevated fruits did not show a steep decline until 120 d after deployment and disappeared at 190 d (Fig. 3). By comparison, ground fruits in 2014 were dispersed within six days of deployment and elevated fruits were taken within 10 d.

DISCUSSION

There were striking between-year differences in all aspects of fruit and seed production and fruit removal by rodents in this *Y. brevifolia* woodland in the western Mojave Desert. These two years appear to represent extremes of fruit production at this site. The number of seeds available for dispersal across the two years was highly variable and depended on fruit crop size, seeds per fruit, and predispersal seed predation. Moreover, rodent abundance, rodent community composition, and the proportions of the fruit crop remaining in the canopy were equally variable across years. Interestingly, these two years of contrasting reproduction occurred during a prolonged drought with rainfall at 43% and 81% of the long-term average in 2013 and 2014, respectively. Although these two years are not consistent with resource matching, they may illustrate another proximate cause of mast reproduction, such as resource accumulation (Meyer and Pendleton, 2015), which depends on the ability to store and reallocate resources when needed for reproduction (Crone and Lesica, 2006; Crone et al., 2009; Sala et al., 2012).

The variability in inflorescence and infructescence production and predispersal seed predation between 2013 and 2014 supports the potential for *Y. brevifolia* to be a masting species. The first year of study was likely a mast year because large numbers of fruits and seeds were produced synchronously and remained in tree canopies for an entire year. In contrast, retention in the fruit-poor year (2014) lasted just two months. Based on reproductive output documented in this study, we calculate a mean of 8.4×10^5 undamaged seeds per hectare were produced in 2013 compared to just 7.6×10^3 per hectare in the low-fruit year. Thus, almost 110 times more seeds were produced in 2013 than in 2014.

Despite the risk of predispersal seed predation associated with yucca moth pollination, unfested fruits had greater numbers of undamaged seeds in 2013, which implies higher fertilization by moths—a result consistent with greater attraction of moths to high-density floral displays in 2013. Greater attraction of moths to the high-density flower displays in 2013 may have resulted in higher fertilization. Thus, variability in floral displays coupled with variation in moth fertilization may promote masting in *Y. brevifolia* (Kelly, 1994). Likewise, predispersal predation by moths was lower

TABLE 2. Densities of inflorescences, infructescences, and fruits per infructescence. Densities are means ± 1 SE for 50 400-m² plots. Fruits per infructescence are means ± 1 SE for 50 random infructescences with the range in parentheses. The percentage of inflorescences producing infructescences is the mean infructescence density divided by the mean inflorescence density.

Year	Inflorescences/400 m ²	Infructescences/400 m ²	Fruits per infructescence	Percent of inflorescences producing infructescences
2013	18.4 \pm 15.9	12.1 \pm 10.9	28.3 \pm 20.8 (1–71)	65.8
2014	5.2 \pm 4.8	2.4 \pm 2.7	8.9 \pm 8.2 (1–31)	46.2

TABLE 3. Undamaged seeds per larval-infested and uninfested fruits, and the percentage of the seeds damaged by moth larvae. Values are means \pm 1 SE. Sample size is in parentheses.

Year	Undamaged seeds/ uninfested fruit	Undamaged seeds/ infested fruit	Percent of seeds damaged by larvae
2013	105.5 \pm 4.9 (40)	84.9 \pm 5.3 (35)	19.5
2014	80.0 \pm 8.6 (13)	45.7 \pm 4.0 (61)	42.8

during the mast year as evidenced by more undamaged seeds per infested fruit. The combination of greater reproduction and lower seed predation in 2013 implies that masting in *Y. brevifolia* may be reinforced by predator satiation prior to seed dispersal.

In the mast year, seed production was high. Fruit fall between 14 and 27 July 2013 resulted in a high number of seeds reaching the ground: an average of 2.85×10^5 undamaged seeds per hectare fell in this 2-wk period. Rapid disappearance of fruits placed on the ground indicates rodents removed and dispersed fallen fruits before turning to the canopy fruits. It was not until 9 September, when fallen fruits became scarce (<10% on the ground, Fig. 3), that rodents began to harvest fruits in the canopy (Fig. 1) and experimentally elevated fruits (Fig. 3). This early focus on fallen fruits likely explains why the number of attached fruits did not change for 50 d, and why the number of rosette fruits changed little for 90 d (Fig. 1). The surplus of fallen fruits during the mast year both delayed and prolonged the harvest of canopy fruits suggesting predator satiation occurred in the year of high-reproduction.

Seed production was low when rodent numbers were high in the nonmast year of 2014. Predispersal insect predation also was much higher (42.8%) than in the mast year (19.5%) and there were fewer fruits and fewer seeds per fruit. In 2014, all fruits were opened or dispersed from the infructescences before they dropped to the ground or into leaf rosettes. In addition, both experimental ground and elevated fruits disappeared within 10 d of deployment, far faster than the 120 d (ground) and 180 d (elevated) in the mast year.

Our findings are consistent with other studies of masting species where reproduction and seed dispersal was compared between mast year and nonmast years. Vander Wall (1997) quantified seed dispersal for single-leaf pinyon pine (*Pinus monophylla*), which has

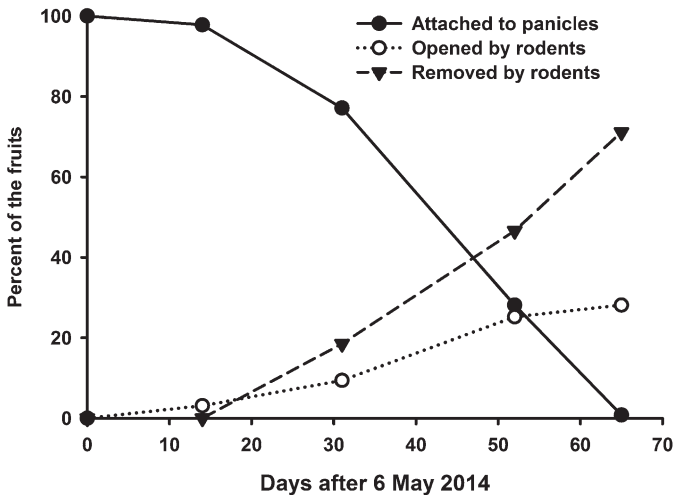


FIGURE 2 Fates of fruits attached to the panicles, opened by rodents, or dispersed by rodents during the low reproduction year of 2014.

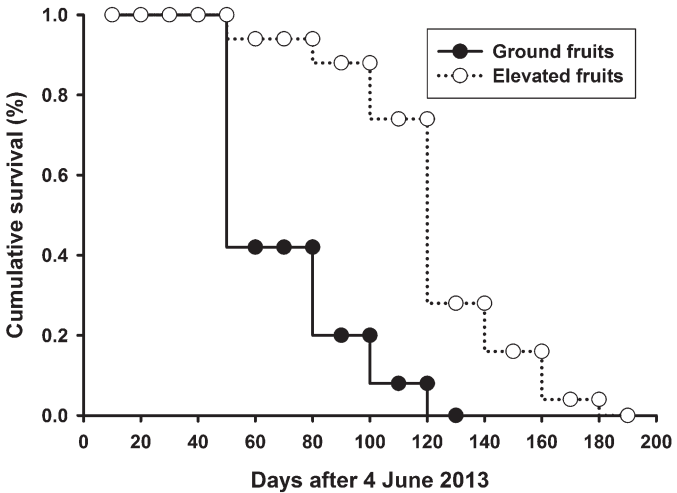


FIGURE 3 Removal of fruits deployed under 50 *Y. brevifolia* plants on the ground and 50 fruits elevated 50 cm above the ground, in 2013.

cones with small flanges on the scales that hinder seed fall as they open. Like pinyon pine, *Y. brevifolia* seeds may remain in infructescences for extended periods. In the year of high pinyon cone production, seedfall continued through the winter and early spring, whereas in the year of moderate cone production, seedfall was limited to a month in the fall. Similarly, we noted that lower *Y. brevifolia* fruit production during the nonmast year of 2014 resulted in rapid seed dispersal during the late spring and early summer, whereas in the mast year, seed dispersal continued for more than a year through the winter and into the spring of 2014.

Yucca brevifolia seeds that were experimentally placed on the ground in this study also mirrored pinyon pine secondary dispersal (Vander Wall, 1997): seeds disappeared slowly in the mast year, but rapidly during the year of lower production. Similar to another masting species, *Prunus armeniaca* (Li and Zhang, 2007), rodent abundance and seed crop size influenced the removal rates of seeds experimentally placed on the ground. They found that seed removal in a year of high seed production and low rodent abundance lasted for months, but in the seed-poor year with high rodent abundance, seeds disappeared within 20 d.

Preliminary camera trapping of six tree canopies in 2014 revealed that both white-tailed antelope squirrels and pinyon mice routinely climbed *Y. brevifolia* trees for fruits (MIB, unpublished data). White-tailed antelope squirrels opened fruits in the canopy, as well as carried them to the ground. Other studies similarly have shown that white-tailed antelope squirrels open canopy fruits and those found on the ground (Zembal and Gall, 1980; Waitman et al., 2012) and that they carry harvested seeds tens of meters from the seed source (Waitman et al., 2012). Both white-tailed antelope squirrels and pinyon mice are efficient seed dispersers (Hollander and Vander Wall, 2004; Beck and Vander Wall, 2010) and were relatively abundant each year, especially in 2014. In addition, both species make numerous caches at depths favorable to seedling emergence (Hollander and Vander Wall, 2004; Beck and Vander Wall, 2010; Waitman et al., 2012).

Pinyon mice are excellent climbers (Laakkonen, 2003) and opened fruits in the canopy, but it was unclear if they carried whole fruits from the canopy to the ground like white-tailed antelope squirrels. Opening of canopy fruits by pinyon mice was likely facilitated by

the low heights of panicles (0.8–2.9 m). In stands with taller trees (5–20 m) pinyon mice may climb less often, or not at all. Like white-tailed antelope squirrels, pinyon mice make numerous single-seed caches (Vander Wall, 1997), often under shrubs (Hollander and Vander Wall, 2004) where *Y. brevifolia* seeds are more likely to germinate and establish as seedlings (Brittingham and Walker, 2000; Reynolds et al., 2012). Finally, seeds in fallen fruits are dispersed by Merriam's kangaroo rats, which, like antelope squirrels and pinyon mice, are avid cachers of *Y. brevifolia* seeds (Waitman et al., 2012).

Of the low-abundance rodent species, desert woodrats, California ground squirrels, and Merriam's chipmunks can climb *Y. brevifolia* to obtain fruit. Desert woodrats are likely exclusively seed predators because seeds carried into their stick houses have almost no chance of becoming seedlings. Both California ground squirrels and Merriam's chipmunks were observed caching Jeffrey pine (*Pinus jeffreyi*) seeds (MIB personal observation), and we hypothesize that they likely disperse *Y. brevifolia* seeds. Hollander and Vander Wall (2004) found that least chipmunks (*Eutamias minimus*) scatterhoard pinyon pine seeds. Agile kangaroo rats (*Dipodomys agilis*) and San Diego pocket mice (*Chaetodipus fallax*) are not climbers, but both probably scatterhoard seeds (Borchert et al., 2003; Hollander and Vander Wall, 2004).

A significant portion of the 2013 fruit crop fell to the ground when fruits were drying or after brief rainfall events. Because canopy fruits and fallen fruits attract different suites of rodent species, the quantity and quality of seed dispersal from these two seed sources likely promotes a diversity of seed-caching species on the ground (Hollander and Vander Wall, 2004; Swartz et al., 2010). The angle of the panicle also influenced the proportion of fruits that fell to the ground. In general, as the angle of the panicle decreased from vertical, the greater the number of fruits fell to the ground instead of into rosettes (MIB, pers. observation). In the study area, where trees are relatively short, 42% of the panicles were vertical, 29% were tilted from 10–30° and 29% were tilted 45° or more. In stands with taller trees (10–20 m) the long, spreading branches may produce more tilted panicles (Gucker, 2006a) resulting in a higher percentage of the crop falling to the ground. Despite lower rodent numbers and decreased species richness during 2013, opportunities for fruit collection and seed dispersal occurred over a longer period of time compared with 2014. Therefore, animal dispersal in 2013 could reinforce masting as reproductive strategy in *Y. brevifolia*, compared with 2014 when fruits were rapidly collected, and potentially consumed, before caching. Additional information about fruit dispersal distances and primary and secondary dispersal by seed-caching rodents is needed to provide support for seed dispersal hypothesis as a factor driving masting in this species.

In addition to *Y. brevifolia*, two other *Yucca* species in southern California have indehiscent fruits with large seeds and are candidates for animal dispersal: *Y. schidigera* and *Y. baccata* (Yeaton et al., 1985; Waitman et al., 2012). *Yucca schidigera* leaf rosettes are elevated (0.5–5 m) on stems, which likely favors visits by climbing rodents (Gucker, 2006b). On the other hand, the leaf rosettes of *Y. baccata* frequently grow at or near the ground (MIB, personal observation), perhaps making fruits more accessible to nonclimbing rodents like kangaroo rats and pocket mice (*Perognathus* and *Chaetodipus* spp.). As yet, it is not known if drying fruits fall of their own weight in these two species.

Regional differences in seedling emergence are important for predicting range-wide opportunities for recruitment, particularly

for long-lived species whose establishment is driven by pulsed-availability of resources. Germination and emergence of *Y. brevifolia* seedlings generally occur in response to heavy precipitation events, and seedlings emerging after summer rains in particular, benefit from prolonged root growth through the fall and winter before soil moisture decreases during the subsequent spring (Reynolds et al., 2012). To compare the opportunities for recruitment at this western Mojave site with those of the eastern Mojave, we calculated the percentage of years in the climate record that had at least one month between July and October receiving >45 mm of precipitation (Reynolds et al., 2012). Based on the 50-yr climate period (1965–2014) generated from PRISM, we would expect favorable emergence for our study site in 14% of the years on record. This infrequent seedling emergence for the western Mojave agrees with Reynolds et al. (2012) and is in stark contrast to the 68% of years that they estimated for emergence opportunities in the eastern Mojave. If summer months are indeed the best period for seedling emergence, there is a high likelihood that viable seeds at our site are available for dispersal and germination, even in the early weeks of fruit-poor years (2014). It should be noted, however, that seed viability declines by as much as 50% after one year in the soil (Reynolds et al., 2012). In contrast, fresh seeds, or those kept in storage, have high germination (90–95%) (Esque et al., 2010; Waitman et al., 2012).

Our study presents the possibility that a portion of seeds produced during mast years may function as a viable aerial seed bank well after fruit maturation. It remains to be seen, however, how long seeds in the canopy are viable and contribute to seedling recruitment after they are scatterhoarded in the soil through time. Future research is needed to explore the relative importance of aerial vs. soil seed banks (Michaletz et al., 2013; Poudner et al., 2014), especially as regional climate variability increases and associated impediments to plant establishment, such as invasive species and wildfires, become more frequent (DeFalco et al., 2010).

ACKNOWLEDGEMENTS

The authors thank S. E. Meyer, P. A. Medica, and two anonymous reviewers for their comments, which significantly improved the final manuscript. This project was partially supported by the U. S. Geological Survey—Ecosystem Mission Area. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U. S. government.

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